# INFRAGENERIC CLASSIFICATION AND NOMENCLATURAL NOTES FOR PYCNANTHEMUM (LAMIACEAE)

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#### ABSTRACT

The history of sectional classifications of *Pycnanthemum* is discussed, and it is proposed to modify the infrageneric arrangement by Bentham (1848) to account for more recent biosystematic studies of the genus. Seven sections are proposed: 1. Sect. *Pycnanthemum*, 2. Sect. *Aristatae*, 3. Sect. *Brachystemum*, 4. Sect. *Capitellatae*, 5. Sect. *Macrocephalae*, 6. Sect. *Nudae*, and 7. Sect. *Californicae*. Each section is based on one diploid species (except 3 in Sect. 1) and may include one or more derived allopolyploid species that most resemble(s) the diploid progenitor(s). Similarities used for sectional assignment of the alloploids are chiefly key features of leaf shape, habit, inflorescence morphology, and chromosome number. Published chromosome counts and hybridization studies have shown the genus to be a hybrid, polyploid, and partly agamospermous complex. Taxa of hybrid origin link the basic diploid species of different sections. The placement of the derived, principally tetraploid, species in one or another parental section involves arbitrary decisions based on the key traits mentioned above. In a reticulate genetic complex such as this, the ideal of a classification with only monophyletic categories is not possible. Our sections are based on the diploid entities that resulted from early divergent evolution in the genus, while the later-formed hybrid and morphologically intermediate taxa are accommodated in the most practical way possible. Lectotypes are designated for the sections proposed by Bentham (1848) and for *Satureja virginiana* L., the basionym of *Pycnanthemum virginianum* (L.) Robins. & Fernald.

#### RESUMEN

Se discute la historia de las clasificaciones seccionales de *Pycnanthemum*, y se propone modificar la ordenación infragenérica de Bentham (1848) para explicar los estudios biosistemáticos más recientes del género. Se proponen siete secciones: 1. Sect. *Pycnanthemum*, 2. Sect. *Aristatae*, 3. Sect. *Brachystemum*, 4. Sect. *Capitellatae*, 5. Sect. *Macrocephalae*, 6. Sect. *Nudae*, y 7. Sect. *Californicae*. Cada sección está basada en una especie diploide (excepto 3 en la Sect. 1) y puede incluir una o más especies derivadas alopoliploides que más se parezcan al progenitor diploide. Las similitudes usadas para la asignación seccional de los aloploides son principalmente características de la forma de la hoja, hábito, morfología de la inflorescencia, y número cromosomático. Los recuentos cromosomáticos publicados y los estudios de hibridación han demostrado que el género es un complejo híbrido, poliploide y parcialmente agamospermo. Los taxa de origen híbrido unen las especies básicas diploides de diferentes secciones. La colocación de las especies derivadas, principalmente tetraploides, en la sección de uno u otro parental implica decisiones arbitrarias basadas en los caracteres clave mencionados más arriba. En un complejo genético reticulado como este, el ideal de una clasificación que sólo tenga categorías monofiléticas no es posible. Nuestras secciones se basan en entidades diploides que resultaron de una evolución divergente temprana del género, mientras que los híbridos formados más tarde y taxa morfológicamente intermedios se acomodan del modo más práctico posible. Se designan lectotipos para las secciones propuestas por Bentham (1848) y para *Satureja virginiana* L., el basiónimo de *Pycnanthemum virginianum* (L.) Robins. & Fernald.

### A PROPOSED SECTIONAL ARRANGEMENT OF PYCNANTHEMUM SPECIES

Up to the time of George Bentham's treatment of *Pycnanthemum* for the *Prodromus* of Alphonse de Candolle (1848), two principal species-groups had commonly been recognized, first as the two genera *Pycnanthemum* and *Brachystemum* by Michaux (1803) and then as Section *Tullia* and Section *Brachystemum* by Bentham (1834). In his more elaborate treatment of 1848, Bentham formally described six sections, to be discussed below. The much later generic monograph by Grant and Epling (1943) did not recognize formal sections, but rather defined two principal groups, termed the Incanum Phylad, of 8 taxa, and the Virginianum Phylad, of 5 taxa. The remaining 8 species were irregularly connected to these groups in a chart (their Figure 1) displaying a network of relationships and suggesting multiple transitional forms and gene exchange between taxa. In their analysis, only *P. californicum* and *P. nudum* "present no transitional forms with other species."

In our previous papers and unpublished work (Chambers 1961a, b; Chambers & Chambers 1971; Chambers 1993) no formal sections of *Pycnanthemum* were recognized, but the taxa were arranged in six informal "species groups." These paralleled the named sections of Bentham but differed in some respects, due

to the addition of several species to the genus after his publication, as well as new information gained from our cytological and hybridization studies. We went beyond Grant and Epling (1943) in not only recognizing their "Incanum" and "Virginianum" phylads, but also in organizing the outlying taxa of their relationship network into arbitrary species groups. Our informal classification is given in Table 1, which lists the known somatic chromosome numbers of each species (Chambers & Chambers 1971).

While Grant and Epling (1943) spoke of transitional forms between species and the possibility that some species were themselves of hybrid origin, our later work (Chambers 1961a, b; Chambers & Chambers 1971, Chambers 1993) has defined the genus as a polyploid complex, with 9 extant diploid species (Table 1), apparent autopolyploidy in *P. albescens*, *P. muticum*, and *P. tenuifolium*, and 10 taxa that are limited to the tetraploid level. The latter appear, for the most part, to be morphologically intermediate between known diploids, such that an alloploid origin is strongly suggested. Accompanying this polyploid evolution in some species has been the development of facultative or obligate agamospermy, marked morphologically by flowers with short filaments and aborted anthers. Where tested in sterile-anthered plants of *P. virginianum*, *P. verticillatum*, and polyploid *P. muticum*, seed-set was normal in both bagged and un-bagged inflorescences (Chambers 1961). Plants with aborted anthers also occur in *P. tenuifolium*, but although apomictic behavior is suspected, it has not yet been checked experimentally (Chambers 1961).

Although it would be desirable to divide the genus entirely into monophyletic sections, we believe that the reticulate nature of evolution in *Pycnanthemum*, involving, as it does, allopolyploidy, a polyphyletic hybrid origin¹ for several widespread taxa, and the preservation of sterile hybrids via apomixis, precludes such a classification at present. Our approach is to propose a practical infrageneric classification involving certain arbitrary decisions about the placement of species that putatively are derived from allopolyploidy or complex polyphyletic hybridity. Basic to our classification is that each section contains one or more of the known sexual diploid species, and no sections are composed only of polyploids (alloploids, complex hybrids, or apomicts). By this plan, we have chosen to place each taxon of suspected hybrid origin into whichever section contains the diploid(s) it most resembles morphologically. This has involved a choice of emphasis on certain key features, especially those of habit, leaf morphology, and details of the inflorescence. An example of this decision process is discussed under *P. setosum*, below.²

Complementing the chromosomal and hybridization research mentioned above have been two recent studies using molecular approaches. The thesis by Yetter (1989) examined relationships in the Virginianum Group, using 12 enzyme systems to identify synapomorphic alleles as well as alleles unique to particular diploid taxa. The work of Williams (2005) developed a cladogram of relationships among all but one species of *Pycnanthemum*, based on sequence data from the ITS region of nuclear ribosomal DNA. (Technical difficulties prevented the inclusion of *P. setosum*. Nominally no *P. clinopodioides* was included in her study, but it may have been represented by a population that she classified as *P. torreyi*)

Our proposed sectional classification takes account of the molecular information from the above research. It emphasizes the nine basic diploid species, using morphological evidence to place each allopolyploid taxon arbitrarily in association with the parent species that it more resembles. The named sections and their included species are presented below, with diploid species in bold-face.

## 1. Sect. Pycnanthemum. Type: Clinopodium incanum L., typ. cons. = P. incanum (L.) Michx.

Syn.: Sect. Tulliae Benth. in DC. Prod. 12:187. 1848. Type: Tullia pycnanthemoides Leavenw. (LECTOTYPE, designated here, Amer. J. Sci. Arts, Ser. 1, 20:343, t. 5, 1831, = P. pycnanthemoides (Leavenw.) Fernald).

Included species.—**P. albescens** Torr. & A. Gray, **P. curvipes** (Greene) E. Grant & Epling, **P. loomisii** Nutt., P. clinopodioides Torr. & A. Gray, P. incanum (L.) Michx., P. pycnanthemoides (Leavenw.) Fernald.

<sup>&</sup>lt;sup>1</sup>A hypothesized origin through numerous, independent hybridization events between different populations of the putative ancestral species.

<sup>&</sup>lt;sup>2</sup>Dr. P.D. Cantino has made the interesting suggestion (pers. comm.) that the problem of classification of hybrids through arbitrary assignment to formal sections might be avoided through the use of PhyloCode nomenclature. In our opinion, a much better developed morphological and molecular cladistic phylogeny for *Pycnanthemum* is needed, before applying PhyloCode methods to the monophyletic groups hypothesized in our studies.

TABLE 1. Informal species groups used in the papers by Chambers and Chambers. Diploid numbers and names of species that are partly or wholly diploid are in bold-face.

Species Group	Included species	Chromosome numbers (2n)	
Incanum Group	P. albescens	<b>38</b> , 76	
	P. loomisii	38	
	P. curvipes	40	
	P. pycnanthemoides	72	
	P. incanum	76*	
	P. clinopodioides	76	
	P. floridanum	78	
Flexuosum Group	P. flexuosum	36	
	P. setosum	76	
Virginianum Group	P. muticum	<b>40</b> , 80, ca. 108	
	P. tenuifolium	<b>40</b> , 80	
	P. pilosum	78	
	P. torreyi	80	
	P. verticillatum	ca. 76–78	
	P. virginianum	80	
Montanum Group	P. montanum	40	
	P. beadlei	76	
Nudum Group	P. nudum	40	
Californicum Group	P. californicum	40	

<sup>\*</sup>The reported count of 2n=78 for *P. incanum* (Chambers 1993) was a misprint for 2n=76.

2. Sect. Aristatae Benth. in DC. Prod. 12:186. 1848. Type: P. aristatum Michx. (Lectotype, designated here, Fl. bor.-amer. 2:8, pl. 33, 1803, = P. setosum Nutt.).

Included species.—P. flexuosum (Walt.) Britton, Sterns & Poggenb. (syn.: P. hyssopifolium Benth.), P. setosum Nutt.

**3. Sect. Brachystemum** (Michx.) Benth., Labiat. gen. spec. 329. 1834. Type: Brachystemum muticum Michx. (LECTOTYPE, effectively designated by Grant & Epling, Univ. Calif. Publ. Bot. 20:202. 1943), = P. muticum (Michx.) Pers.).

Syn.: Sect. Mutica Benth. in DC. Prod. 12:188. 1848. Type: Brachystemum muticum Michx. (LECTOTYPE, designated here, Fl. bor.-amer. 2:6, pl. 32. 1803, = P. muticum (Michx.) Pers.).

Included species.—P. muticum (Michx.) Pers., P. beadlei (Small) Fernald, P. floridanum E. Grant & Epling.

**4. Sect. Capitellatae** Benth. in DC. Prod. 12:189. 1848 (as Capitellata). Type: Brachystemum lanceolatum Willd. (LECTOTYPE, designated here, Willdenow, Enum. pl. 623.1809, = P. virginianum (L.) Robins. & Fernald).

Included species.—**P. tenuifolium** Schrad., P. pilosum Nutt., P. torreyi Benth., P. verticillatum (Michx.) Pers., P. virginianum (L.) Robins. & Fernald.

- **5. Sect. Macrocephalae** Benth. in DC. Prod. 12:189. 1848 (as "Macrocephala"). Type: P. montanum Michx. Included species.—P. montanum Michx.
- 6. Sect. Nudae Benth. in DC. Prod. 12:189. 1848 (as "Nuda"). Type: P. nudum Nutt.

Included species.—P. nudum Nutt.

7. Sect. Californicae K.L. Chambers & H.L. Chambers, sect. nov. Type: P. californicum Durand, J. Acad. Nat. Sci. Philadelphia Ser. II, 3:99. 1855.

Plantae superne albo-tomentosae foliis subsessilibus cordatis vel truncatis ovatis acutis denticulatis floribus capitatis terminalibus et in axillis bractearum dispositis bracteis foliaceis bracteolis capitulorum erectis angustis calicibus equidentatis dentibus triangulatis dense tomentosis corollis maculatis staminibus exsertis.

Included species.—P. californicum Durand.

Lectotypes are proposed, above, for the sections of Bentham containing more than one species. As noted, the genus *Brachystemum* was earlier typified by Grant and Epling (1943) with *B. muticum*, so Bentham's Section *Mutica* becomes superfluous. For Sect. *Capitellatae*, of the two species cited by Bentham we have elected Willdenow's (1809) *B. lanceolatum* (= *P. virginianum*) as the type rather than his *B. linifolium* (= *P. tenuifolium*), because the latter name is illegitimate, and Willdenow's description is at variance with the type and description of *Satureja virginiana* L., the origin of his cited synonym *Thymus virginicus* L. (1771).

Section *Pycnanthemum* is the only section containing more than one diploid species. Its members are characterized by loose, well-branched flower clusters, both terminal and (often) in the axils of 1–4 bracteate leaf pairs below this. Leaves are broad, petiolate, and often canescent on one or both sides, especially distally on the plant. We hypothesize that this section contributed to the origin of intersectional alloploids showing a tendency toward relatively tight but visibly branched flower clusters, for example *P. beadlei*, *P. floridanum*, and *P. pilosum*, the other putative parents having tight capitula.

We follow Bentham (1848) in placing *P. flexuosum* in Sect. *Aristatae*, in association with its very likely allotetraploid derivative *P. setosum* (see chromosome pairing of 19 IIs and 18 Is at meiosis in triploid backcross hybrid #75, Chambers 1993). The other putative parent of *P. setosum*, *P. muticum*, is in Sect. *Brachystemum*. An alternative would be to create a monotypic section for *P. flexuosum* and leave *P. setosum* alone in an alloploid Sect. *Aristatae*, but this goes against our plan to have each section contain at least one diploid species. Additionally, it would create a precedent for other alloploid species like *P. floridanum*, *P. beadlei*, *P. virginianum*, et al., to be segregated into monotypic sections of their own. The resemblance of *P. setosum* to *P. flexuosum* is expressed in features of stem puberulence, distinct branchlets in the capitula, aristate inflorescence bractlets, reduced calyx pubescence, and calyx teeth acuminate with an aristate tip up to 1 mm long. Especially in the northern portion of its range, *P. setosum* often resembles its other putative parent *P. muticum* in traits of habit (general absence of leafy, sterile side-branches), leaf shape (more broadly lanceolate leaves), and upper bracteate leaf pair subtending the capitula (reduced, ovate, canescent, and often drooping). Besides its morphological intermediacy, *P. setosum* has 2n=76, which is the sum of the diploid numbers of the putative parental species.

Section Brachystemum, centered on diploid P. muticum, also provides other examples of alloploid species being included, by choice, with one of their likely diploid ancestors. A relationship of tetraploid P. floridanum to P. muticum, as is suggested by the DNA data of Williams (2005), implies that the gametic number n=39 in P. floridanum must include a 20-chromosome genome derived from P. muticum. On morphological and cytological grounds, P. floridanum's other diploid parent is probably a species with n=19 in Sect. Pycnanthemum (as predicted by Grant and Epling 1943, p. 210, referring to their Incanum Phylad). One candidate taxon is P. albescens, but this possible relationship has not yet been tested experimentally. In a further example, P. beadlei, another tetraploid, has traditionally been associated taxonomically with P. montanum (they are sympatric in the southern Appalachians). However, Williams' DNA data from nuclear ribosomal ITS genes (2005) do not support a close phylogenetic relationship between the two. Instead, P. beadlei appears in a clade with P. muticum and some of its other tetraploid derivates. The chromosome numbers of n=38 in the former species and n=20 in the latter suggest that a second genome of 18 occurs in P. beadlei, perhaps from an ancestral diploid in Sect. Pycnanthemum, where x=18 is known (although no extant species have n=18). Artificial hybrids #12 and #15 between P. beadlei and P. muticum (Chambers 1993) showed up to 20 chromosome pairs and 18 singles at first division of meiosis in pollen-mother cells. Pycnanthemum beadlei is therefore assigned to Sect. Brachystemum.

Section Capitellatae contains the core of the earlier Virginianum Complex, which we view as comprising *P. tenuifolium* plus hybrid derivatives of that taxon with members of one or more other sections. *Pycnanthemum tenuifolium* is distinguished by its linear leaves, numerous small and compact floral heads, bractlets of the heads acuminate, pungent, and arcuate basally, with stout, emergent midnerve, and a bushy habit due to numerous vegetative branches arising from the stem nodes. In the derived tetraploid species *P. virginianum*, *P. pilosum*, *P. torreyi* and *P. verticillatum*, the leaves are usually lanceolate, the heads somewhat looser (espe-

cially *P. pilosum*), the capitular bractlets less pungent (though still with a notably stout midnerve), and the habit frequently less bushy. There is good molecular evidence that the broader leaves, less-branched habit, and non-pungent bractlets came from the second parent of many tetraploid forms, namely *P. muticum* (Yetter 1989; Williams 2005). From his allozyme studies, Yetter concluded: "Tetraploids traditionally labeled *Pycnanthemum virginianum* and *P. pilosum* are thought to be allopolyploid derivatives of diploid *P. muticum* and *P. tenuifolium* as indicated by the possession of alleles which are unique to the diploids" (1989, p. 80). In the DNA analyses by Williams (2005), samples of the alloploid taxa *P. virginianum*, *P. pilosum*, and *P. verticillatum*, of Sect. *Capitellatae*, were always associated in her cladograms with *P. tenuifolium* or *P. muticum*, not with species from other sections. Additional evidence comes from the artificial diploid hybrid of *P. muticum* × *P. tenuifolium* (#84, Chambers 1993). In the morphology of habit, leaves, and floral capitula, this hybrid can easily be classified as *P. virginianum* (voucher OSC 192224). Our assignment of *P. muticum* to the separate Sect. *Brachystemum* recognizes its involvement in other intersectional hybrids in addition to those involving *P. tenuifolium*. Finally, we differ from Bentham (1848) in placing *P. torreyi* in the same section as *P. tenuifolium* rather than with *P. muticum*, but this is tentative awaiting further study, since DNA evidence suggests that *P. torreyi* is itself of complex, polyphyletic hybrid origin (Williams 2005).

The monotypic sections *Macrocephalae*, *Nudae*, and *Californicae* are not at this point implicated in the origin of any polyploid taxa. However, intersectional hybrids have been produced artificially (Chambers & Chambers 1971; Chambers 1993), and a natural hybrid of *P. nudum* × *P. flexuosum* has been described (Chambers & Chambers 1971). Hybrids with mostly sterile pollen have been produced in crosses of *P. muticum* × *P. montanum*, *P. muticum* × *P. tenuifolium*, *P. flexuosum* × *P. nudum*, *P. flexuosum* × *P. tenuifolium*, and *P. flexuosum* × *P. loomisii* (Chambers 1993). Puzzling intermediate forms will no doubt be found in nature involving these and other species, such that species boundaries, especially at the tetraploid level, will be blurred (Grant & Epling 1943, pp. 233–236). Even if sterile, such hybrids may occasionally persist through seed apomixis or vegetative clonal reproduction.

Our revised sectional classification of *Pycnanthemum* is summarized in Table 2. A taxonomic treatment of the genus is in preparation for inclusion in a future volume of *Flora of North America* (Flora of North America Editorial Committee, 1993 onwards).

### LECTOTYPIFICATION OF PYCNANTHEMUM VIRGINIANUM L.

There are three species named by Linnaeus in *Species Plantarum* (1753) that today are placed in the genus *Pycnanthemum*. These are *Satureja virginiana* (p. 567), *Nepeta virginica* (p. 571), and *Clinopodium incanum* (p. 588). *Clinopodium incanum* L., now *Pycnanthemum incanum* (L.) Michx., is the conserved type of the genus (Rickett & Stafleu 1960; McNeill et al. 2006). It was lectotypified with a Kalm specimen, Herb. Linn. No. 742.4, by Reveal et al. (1987, see Jarvis 2007, p. 428). We would not hazard a guess as to why Linnaeus cited "*Habitat in Europa boreali*" for this strictly North American species.

The name Satureja virginiana (Linnaeus 1753, p. 567) has since 1908 or before been treated in all North American floras as the basionym of Pycnanthemum virginianum (L.) Robins. & Fernald, a common and widespread taxon in eastern North America. Its lectotypification has been uncertain, in part because some of the pre-Linnaean polynomials cited in the original description are known to refer to the related species, P. tenuifolium Schrad. (Epling 1929; Grant & Epling 1943; Jarvis 2007). Epling (1929) at first suggested that P. virginianum was synonymous with P. linifolium (Willd.) Pursh, a synonym of P. tenuifolium. However, in Grant and Epling (1943) he changed his mind, saying that Linnaeus had in his herbarium a specimen of what we today know as P. virginianum, and because this usage "has now become well established....it seems preferable not to make another change." Epling did not formally propose the Linnaean Herbarium specimen as a lectotype, however. This specimen is Herb. Linn. 744.21. It is annotated in Linnaeus' script "Sat[ureja] 1 virginiana" and reannotated by Smith "Sp. Pl. 1. Pycnanthemum linifolium Sm. in Rees's Cyclop." It is filed as sheet number 21 under the genus Thymus (Savage 1945).

We have examined the excellent image of this sheet available through the Linnaean Herbarium website

Table 2. Sections of *Pycnanthemum* and their included species, as here proposed. Bold-face indicates species that are partly or wholly diploid.

Section	Species	
1. Pycnanthemum	P. albescens	572 
	P. clinopodioides	
	P. curvipes	
	P. incanum	
	P. loomisii	
	P. pycnanthemoides	
2. Aristatae	P. flexuosum	
	P. setosum	
3. Brachystemum	P. beadlei	
	P. floridanum	
	P. muticum	
4. Capitellatae	P. pilosum	
	P. tenuifolium	
	P. torreyi	
	P. verticillatum	
	P. virginianum	
5. Macrocephalae	P. montanum	
6. Nudae	P. nudum	
7. Californicae	P. californicum	

(<www.linnean.org>), and we find that it is undoubtedly a specimen of *Pycnanthemum virginianum* as that name has been applied in North America for the last 100 years. There are certain details in Linnaeus' description of *Satureja virginiana* that aptly fit this specimen but that are inappropriate for *P. tenuifolium* (the other species to which "virginiana," or the variant "virginica," have been applied). Firstly, Linnaeus described the leaves as "foliis lanceolatis," and in citing his earlier polynomial from *Hortus Cliffortianus* (Linnaeus 1737, p. 305), he changed the "foliis linearibus acuminatis" from that work to "foliis lanceolatis acuminatis," presumably better to fit the specimen he had at hand. Secondly, this specimen has tiny stamens and clearly represents the agamospermous form of *P. virginianum* which is the common type found in the Atlantic Coast states (Chambers 1961a). These non-functional stamens are well described by Linnaeus in his observation, "Stamina in fundo corollae latent Antheris minimis effoetis, ut fere posset genere proprio tradi." This differs from *P. tenuifolium*, which in this same region reproduces sexually and has exserted stamens with functional anthers (Chambers 1961a).

Therefore, based on these considerations, we here designate Herb. Linn. 744.21 (LINN) as the lectotype of *Satureja virginiana* L., Sp. Pl. 1:567. 1753.

The difficult case of the name *Nepeta virginica* L., which also lacks lectotypification, is under study by James Reveal and Charlie Jarvis (pers. comm.), and their recommendation will be published in due course. The epithet "virginica" is not available in *Pycnanthemum*, due to the preexisting *P. virginicum* (L.) Pers. (1806) based on *Thymus virginicus* L. (1771).

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<sup>&</sup>lt;sup>3</sup>Translated by us as, "Stamens lie hidden in base of corolla Anthers very small exhausted, such as hardly ever can bequeath proper offspring."

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